



Changes of plant species composition in the Šumava spruce forests, SW Bohemia, since the 1970s[☆]

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Received 3 September 2001; received in revised form 30 January 2003; accepted 27 June 2003

Abstract

Vegetation dynamics of three forest communities were studied by resampling of relevés recorded in the 1970s in the Bohemian Forest (Šumava Mountains). Results of multivariate analysis (RDA) confirmed significant time changes in species composition of the climax (*Calamagrostio-Piceetum*) and waterlogged (*Bazzanio-Piceetum*) spruce forests. The changes in the sphagnum-rich waterlogged spruce forests (*Sphagno-Piceetum*) are close to the level of significance. The main vegetation changes are represented by a decrease in cover and/or frequency of hygrophilous or sciophilous species (e.g. *Athyrium distentifolium*, *Oxalis acetosella*) in climax spruce forests, and an abundant increase of species, indicating a preference to drier stands or better light conditions (e.g. *Calamagrostis villosa*, *Vaccinium vitis-idaea* or *Avenella flexuosa*), in waterlogged spruce forests. We also found a higher proportion of meadow species (e.g. *Anthoxanthum odoratum*, *Festuca rubra* or *Luzula multiflora*) in the newly recorded relevés from waterlogged forests. Analysis of species number per plot showed a remarkable shift to species-rich communities, especially in waterlogged stands.

We tried to find the possible factors responsible for the observed changes. Unfortunately, only indirect measurement of environmental factors using Ellenberg's indicator values could be used and did not yield sufficient results. Thus, the changes observed in climax spruce forests were ascribed mainly to a decrease in canopy cover, which was directly estimated. In waterlogged forests, a complex of several general factors, which influence the climax spruce forest, had to be taken into account, such as: (i) a decrease in atmospheric acidification during the last 10–15 years and subsequent improvement in soil conditions, especially in waterlogged stands; (ii) fragmentation of forests as a result of bark-beetles attack; (iii) climate warming documented by long-term local meteorological measurements.

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Keywords: Vegetation dynamics; Time changes; Bohemian Forest; Czech Republic

1. Introduction

The dynamics of forest communities, which are highly endangered in some areas of the Czech Republic,

have been studied with respect to environmental changes. Spruce stands of the Bohemian Forest (Šumava Mountains) have recently fallen into this category.

These studies have been carried out in Scandinavia where forests cover a major part of the area (cf. Bohn et al., 2000) and paying particular attention to spruce and pine stands (see, e.g. Brakenhielm and Persson, 1980; Engelmarm et al., 1998; Hofgaard, 1993;

[☆] For nomenclature of vascular plants, see Ehrendorfer (1973), for bryophytes Frahm and Frey (1992), and for lichens Poelt (1969).

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Økland, 1994, 1995; Økland and Eilertsen, 1996). Most studies have followed the impact of air pollution on changes in the occurrence and abundance of plants. Detailed attention has also been paid to changes in species composition in the ground layer that plays an important role in these forests (cf. Økland, 1995; Lähde and Nieppola, 1987; Nygaard and Ødegaard, 1999). In the Czech Republic, on spruce and spruce–beech forest (Vacek and Lepš, 1991, 1992) changes due to the emission impact on N Bohemia were closely followed.

The Bohemian Forest has been a target of frequent phytocoenological research since the 1920s. The first studies were mainly dedicated to non-forest vegetation (mires, mat-grass meadows). Since the end of the 1950s, valuable forest communities were also studied, and later followed by other vegetation types (see Sofron, 1969, 1984). Recent biological, hydrological and forest research is concentrated mostly in the area of the Šumava National Park and the results published in the journal *Silva Gabreta*, Vimperk. Though many studies have been devoted to the spruce forest vegetation of Bohemian Forest (e.g. Sofron, 1981; Kučera in Pecharová and Rada, 1995; Sofron and Štěpán, 1971; Jirásek, 1996; Neuhäuslová and Eltsova, 2001, 2002), no study has analysed vegetation changes in this area.

In 1999, research on the diversity and dynamics of the spruce stands in the Bohemian Forest started. The character of the mountains, which were described at the beginning of the 1990s as a “more-or-less continuous island of forests” (Hladilín, 1996) changed significantly in some places during subsequent years. Significant damage and destruction of vast forest areas occurred in the central frontier part of the Bohemian Forest, especially in the area of large spruce plantations surrounding the villages of Kvilda and Modrava, gamekeeper’s house at Březník, the water reservoir at Roklanská nádrž and Lusen Mountain. Even-aged plantations of spruce, sometimes of unknown origin, are unable to resist to air pollution, snowbreaks and windfall following bark-beetle attack (mostly *Ips typographus* and other species of xylophagous insects). These disturbances are among the causes of diminishing forest stands, not only in the Bohemian Forest (Zelenková et al., 2000), but also in other mountains of the republic.

The aim of this contribution is to consider (1) the extent of the changes in species composition in three

types of the spruce forests, particularly in the Šumava National Park and the adjoining part of the Šumava Landscape Protected Area, from the 1970s to present, and (2) the causes of these changes.

2. Material and methods

2.1. Study area

The study area includes all of the Šumava National Park (68 064 ha) and the adjoining part of the Šumava Protected Landscape Area in the northwest, i.e. the Královský Hvozd ridge, including the Pancíř and Můstek mountains in the northwestern frontier part of the Bohemian Forest on the southwestern border of the Czech Republic (see Fig. 1). This area is formed by Moldanubicum rocks (paragneisses and migmatites prevailing) and moldanubicum pluton represented by several broader granite massives. From the quaternary sediments, the deluvial slope deposits of solifluction origin prevail. They represent a rather heterogeneous set of substrates with various thicknesses of the block deposits. Peat is abundant and sediments of glacial origin are scarce.

The Bohemian Forest belongs to the oldest mountains in central Europe with large-scale relicts of plateau above 1000–1100 m altitude. In comparison with other mountains in the Czech Republic, it has a more moderate climate and a high mean altitude, only exceptionally lower than 600 m. The highest peaks on the Bavarian side reach over 1400 m. Annual precipitation varies between 1000 (Kvilda, 1058 m about sea level) and 1300 mm (Prášíly, 850 m a.s.l.) in our study area. The mean annual temperature ranges from 4.2 (Churáňov, 1122 m a.s.l.) to 5.9 °C (Kašperské Hory, 780 m a.s.l.). Podsoles prevail at higher altitudes; spodo-dystric cambisols are also common, while rankers and histosols or lithosols are more rare (see Zelenková et al., 2000).

2.2. Data sampling

Sofron (1981) recorded most phytocoenological relevés in 1972, a few in 1970 and 1976. These relevés were used as a basis for the evaluation of the spruce forest changes. The localities of these recorded relevés, which could be properly identified, were repeatedly

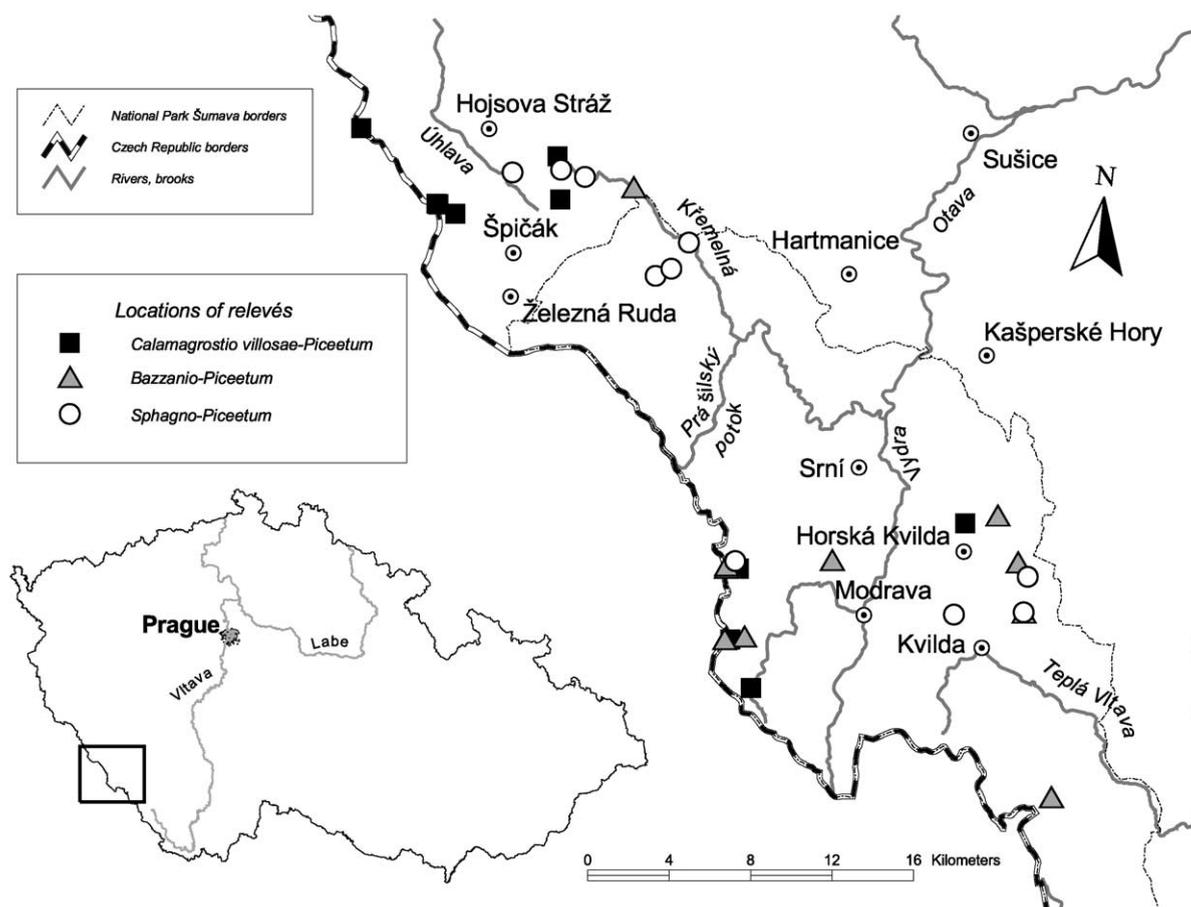


Fig. 1. Location of the resampled relevés in Natural Park Šumava and nearby surroundings.

recorded in 1999 by Neuhäuslová and Sofron. In order to be consistent with the methodology to these workers, an 11° dominance–abundance scale by Domin (Domin ex Krajina, 1933a,b) was also used to record the new relevés. For further evaluation, this scale was then converted to the (Braun-Blanquet, 1964) scale by means of a table by Dahl and Hadač (1941). A total of 28 relevés were repeatedly recorded — 9 in *Calamagrostio villosae-Piceetum* (incl. *Vaccinio myrtillo-Piceetum* and *Deschampsio-Piceetum* sensu Sofron, 1981), 10 in *Bazzanio-Piceetum* (= *Mastigobryo-Piceetum*), and 9 in *Sphagno-Piceetum*. Areas where the forests were replaced by substitute clearing communities, or spruce stands with dead trees were not recorded. The position of the relevé centre was localised by GPS with sub-meter horizontal accuracy. The age of the analysed stands was over 100 (120) years.

The sites of the following relevés by Sofron (1981) were chosen for repeated recording:

- *Calamagrostio villosae-Piceetum* (incl. *Deschampsio flexuosae-Piceetum* and *Vaccinio myrtillo-Piceetum* sensu Sofron, 1981): 7, 8, 18, 20, 24 in Table 1, pp. 32–33, rel. 31 in Table 2, p. 43, rel. 32, 34, 36 in Table 3, pp. 46–47;
- *Bazzanio-Piceetum*: rel. 47, 48, 49, 54, 63, 67, 68, 69, 76, 77 in Table 5, pp. 62–65, and
- *Sphagno-Piceetum*: rel. 82, 83, 85, 87, 88, 91, 97, 98, 106 in Table 6, pp. 70–73.

Stands classified as belonging to *Calamagrostio villosae-Piceetum* are mostly under management. However, we did not suppose any strong intervention (cutting, planting) in the last 30 years, with the exception of one stand (Jezerní Mountain) with sporadic new

plantation. (With respect to the small number of samples, we decided to also include this debatable sample.) Our assumption is based on the characteristics of the analysed stands and the knowledge that forest management activities are mostly oriented to younger stands. The other stands classified into the remaining two syntaxa can be taken as natural, without any activities related to forest plantation. The area of resampled relevés was the same as that of the corresponding original relevés (100–400 m²).

2.3. Data analysis

Time changes in the particular spruce communities and species turnover were tested by redundancy analysis (RDA, covariance matrix — option “Centre and Standardise” in CANOCO for Windows program). The (Braun-Blanquet, 1964) cover scale was converted into corresponding values, e.g. 1 into 1, 2 into 2 and small values were converted as follows: $r = 0.1$; $+ = 0.5$. For a detailed description of the problems related to cover data transformation, see van der Maarel (1979). The use of linear ordination methods was supported by the length of gradient in DCA analysis (less than 3 S.D. units for all three data sets). The cover values of all three vegetation layers were analysed together. The sets of sample plots for the individual communities were analysed separately. All sample plots and all species were active in the analysis. We did not down-weight the species with low frequency but for the interpretation of changes only species with occurrence in more than three relevés were used.

The age of the relevés was treated as an environmental variable and each pair of relevés (i.e. sample plots) as covariables. Permutations were conditioned by covariables. Changes in abundance and species composition were assessed from the species scores on the first axis. The ordination was performed by CANOCO for Windows package (Ter Braak and Šmilauer, 1998).

The presence of successional trends according to ordination axes was tested by comparing sample scores between the years. Detrended correspondence analysis (DCA) was used in this case and the samples from all three communities were analysed together. The comparison of the scores was done by non-parametric Wilcoxon’s paired signed-rank test (Zar, 1999). Species diversity was calculated from the species

cover as a Shannon–Wiener index (Begon et al., 1990). The original Braun-Blanquet scale values were transformed as follows: $r = 0.1$, $+ = 1$, $1 = 2.5$, $2 = 15$, $3 = 37.5$, $4 = 62.5$, $5 = 87.5$.

Main environmental factors were estimated indirectly using Ellenberg’s indicator values (Ellenberg et al., 1992) for light, temperature, moisture, soil reaction and nitrogen. Data for nitrogen were available for higher plants only. Mean values were calculated for each relevé using the Braun-Blanquet scale after transformation to 1–7. To test the shift of ecological factors, mean sample indicator values for each relevé were compared between the years. With the aim to visualise the changes of environmental factors, species indicator values were correlated with species scores on the first RDA axis, which represents the time scale.

Differences between cover of the vegetation layers, as well as those of species number and species diversity, were also analysed by non-parametric Wilcoxon’s paired signed-rank test. The Braun-Blanquet cover values were similarly converted to calculate diversity indices and summed over all species in particular layers.

Data processing was carried out with the SPSS program, version 10.0.5 (SPSS, 2000).

3. Characteristics of the analysed spruce communities

3.1. *Calamagrostio villosae-Piceetum* Hartmann in Hartmann and Jahn (1967)

This syntaxon (incl. *Deschampsio flexuosae-Piceetum* Hadač et al., 1969; *Oxalido-Piceetum* Krajina, 1933a,b; Březina et Hadač in Hadač et al., 1969; *Vaccinio myrtilli-Piceetum*, Szafer et al., 1923; Sofron, 1981) is the most frequent in the area studied. It includes stands with dominant spruce, at present almost the only tree- and shrub-layer species in prevailing plantations. In near-natural stands, *Sorbus aucuparia*, *Fagus sylvatica* or *Abies alba* occur. However, their occurrence is very rare in the central part of the Šumava National Park, due to forest management and high number of deer. *Calamagrostis villosa*, *Avenella flexuosa*, *Luzula sylvatica* or *Vaccinium myrtillus* dominate the species-poor field layer. *Dryopteris dilatata*, *Oxalis acetosella* and *Trientalis europaea* occur

frequently, but with low abundance. The ground layer is usually rich in species; most common are *Dicranum scoparium*, *Polytrichum formosum* and *Sphagnum girgensohnii*, sometimes *Rhytidiadelphus loreus* (cf. also Jirásek, 1996; Jirásek in Husová et al., 2002).

3.2. *Bazzanio-Piceetum* Br.-Bl. and Sissingh in Braun-Blanquet et al. (1939)

Edaphically and microclimatically influenced waterlogged spruce forests poor in higher plants but with a species-rich ground layer, occur at montane and submontane levels. The canopy is usually formed by spruce only. Here and there, *Betula pubescens* (incl. *Betula carpatica*), *Pinus sylvestris* or *P. rotundata*, and rarely regenerating beech are admixed. The field layer is dominated by several more-or-less constant species (*V. myrtillus*, *Vaccinium vitis-idaea*, *A. flexuosa*, *C. villosa*, *D. dilatata*). In the ground layer, dominated by *Bazzania trilobata* (rarely *S. girgensohnii*) frequently covering large areas, more than 20 bryophytes were often recorded. The diagnostic species *B. trilobata* also occurs in another spruce forests syntaxa, however, with much lower abundance.

3.3. *Sphagno-Piceetum* (R. Tüxen 1937) (Hartmann, 1953)

Open, stunted stands (cover 50–60%), often with insufficient differentiation of tree and shrub layers, are found in the marginal zone of the peatlands. Dominant spruce with an occasional admixture of *P. sylvestris*, *P. rotundata* and/or *B. pubescens* s.l., poorly developed field layer containing the most common *V. myrtillus*, *V. vitis-idaea*, *Eriophorum vaginatum* and *Oxycoccus palustris*, and dense cover of the ground layer with prevailing *Sphagnum* species are typical. *Vaccinium uliginosum*, *Carex rostrata* or *Equisetum sylvaticum* occur rarely, but with high dominance in spots. From the bryophytes, *Sphagnum recurvum* s.l. and *Polytrichum commune* prevail. Sometimes, *Sphagnum magellanicum*, *Sphagnum russowii*, *S. cuspidatum* or *S. riparium* occur with high dominance. In the individual stands, the spruce trees are of different age ([50] 80–150 years); the sub-layer trees are often dead. This unit occupies the most extreme sites where the spruce is limited in its growth by excessive water-logging on the old bogs of different thicknesses.

4. Results

4.1. Species composition

Resampling of spruce forests recorded in the 1970s (Sofron, 1981) in the Bohemian Forest showed high variation in species cover and frequency, reflecting high site heterogeneity in the three communities analysed. The heterogeneity between plots (treated as covariables) explained always more than 50% variability in data set (Table 1). After removing the plot effect (using permutation by blocks defined by plots), the RDA revealed significant time changes in species composition (Table 1) in climatic and *Bazzania*-rich spruce stands. The changes in waterlogged stands of the *Sphagno-Piceetum* are close to the level of significance 5% ($P = 0.06$). The response of individual species to time, treated as an environmental variable, indicates scores on the first canonical axis (see Appendix A). The cover or abundance of species with negative scores decreased in time and vice versa. The changes in cover and abundance of individual species are discussed in the next section.

The difference in species composition between communities and its shift during the analysed period was visualised in DCA ordination space (Fig. 3). The samples are clearly differentiated to three communities according to the first axis, which could be explained by moisture gradient. The observed pattern according to the second axis cannot be explained by a single factor.

Table 1
Characteristics of RDA analysis for three different forest communities^a

Community	Covariables variability	First axis variability	F	P
<i>Calamagrostio-Piceetum</i>	56.5	16.9	1.629	0.009
<i>Bazzanio-Piceetum</i>	51.3	17.5	1.915	0.004
<i>Sphagno-Piceetum</i>	52.5	12.5	1.146	0.060

^a Covariables variability indicates the percentage of variability explained by the heterogeneity between locations. (The sample plots were treated as covariables.) First axis variability indicates percentage variability explained by first canonical RDA axis after fitting covariables. Time was treated as a single environmental factor. Significance was estimated using the Monte Carlo permutation test.

The analysis of shift in sample position in ordination space over all communities did not reveal any general successional trend in species composition according to the gradients described by the two DCA axes. The pairwise comparison of sample scores of original and new relevés on the first and second DCA axes, respectively, between the two samplings (T2–T1) was not significant for any community compared.

4.2. Cover and frequency of particular species

4.2.1. *Calamagrostio villosae-Piceetum*

The decrease in both cover and frequency of the hygrophilous species or species of dense canopy *Athyrium distentifolium* and *O. acetosella*, and the higher dominance and increase in frequency of spruce (shrub and field layer) is remarkable providing evidence of good regeneration. Notable is that the relatively frequent occurrence of *Galium saxatile* missing in the 1970s and providing evidence of its invasion beginning on the suitable forest sites in the area of the Bohemian Forest. A somewhat higher proportion of *D. dilatata* and *L. sylvatica* in the stands was also recorded compared with the 1970s. From the bryophytes, only a higher proportion of *D. scoparium* and *S. girgensohnii* was observed.

4.2.2. *Bazzanio-Piceetum*

An increase in dominance and frequency can be seen in many acidophilous species, typical of central European spruce or spruce–beech forests of the submontane to supramontane levels (partly occurring in subalpine grasslands, too). Of these species, *Picea abies* (both shrub and field layers), *S. aucuparia*, *A. flexuosa* and *D. dilatata* (field layer) must be mentioned, as well as *V. vitis-idaea* and *Lycopodium annotinum*, where the increase in frequency is less marked. Also, a number of spruce-forest species such as *C. villosa* (at present occurring very frequently in clearings of the highest altitudes) and *Homogyne alpina* increased. Bryophyte species of waterlogged spruce forests and peatlands (*Sphagnum* species, e.g. *S. girgensohnii*, *S. magellanicum*) as well as *D. scoparium*, *Ptilidium ciliare*, *B. trilobata* and *Dicranodontium denudatum* increased in abundance. On the other hand, the frequency of some bryophytes (*Sphagnum capillifolium*, *Cephalozia lunulifolia*) decreased.

4.2.3. *Sphagno-Piceetum*

Differences in this community concern mainly higher abundances of *A. flexuosa*, *V. vitis-idaea*, *T. europaea*, *C. villosa*, and *V. uliginosum* in the field layer, as well as more frequent occurrence and cover of *P. abies* in the shrub layer and *B. pubescens* agg. in the tree layer (Appendix A). On the other hand the decrease in *Deschampsia caespitosa* and that in cover of hygrophilous *Sphagnum* species (*Sphagnum fallax*, *S. russowii*) must be mentioned.

4.3. Species richness and diversity

The analysis of number of species per plot calculated over all communities (Fig. 2) and in detail for each community and vegetation layer (Table 2) showed a striking shift to more species-rich communities. Species numbers calculated over all vegetation layers were significantly higher in 1999 in all three communities (Table 3). Consequently, vegetation diversity in all three communities also increased significantly with species richness (Table 4). Comparison of particular vegetation layers revealed a significant increase in species numbers only in the field layer in *Sphagno-Piceetum* and in the ground layer in the two waterlogged spruce forests.

4.4. Layer cover

Opening of spruce canopies indicated by a significant decrease of tree-layer cover was found only in

Table 2

The total number and number of retreated or emerged species during time, counted over all relevés within particular communities (species occurring in two or more relevés only are included)

Community	Total no. of species		No. of species	
	1970s	1999	Retreated	Emerged
<i>Calamagrostio-Piceetum</i>				
Field layer	16	20	2	6
Ground layer	13	17	4	8
<i>Bazzanio-Piceetum</i>				
Field layer	14	16	3	5
Ground layer	27	30	9	12
<i>Sphagno-Piceetum</i>				
Field layer	35	49	8	22
Ground layer	20	30	6	16

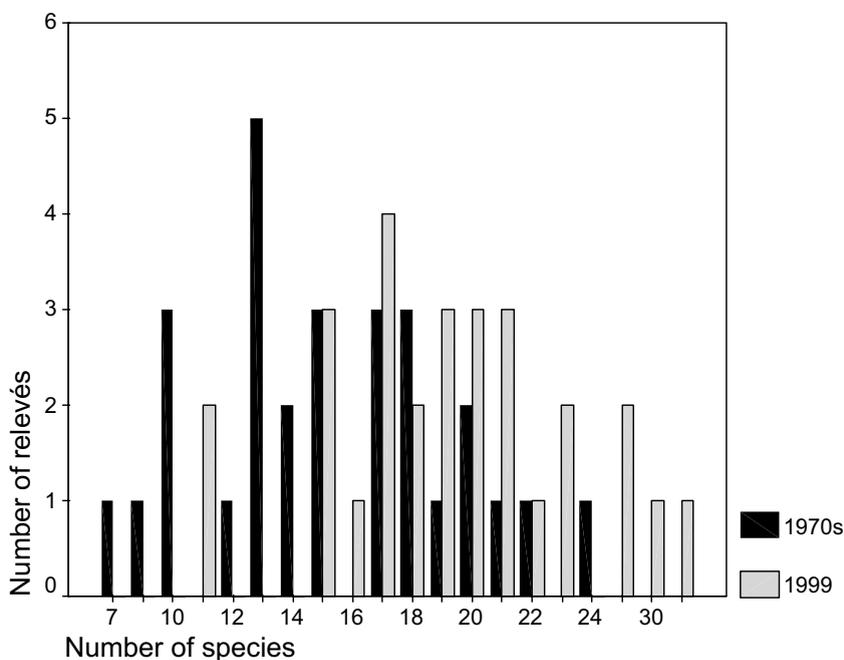


Fig. 2. Time changes in the distribution of number of species per plot over all communities ($P < 0.01$, Mann–Whitney test, $n = 58$).

climatic spruce stands (*Calamagrostio villosae-Piceetum*) (see Table 5). The mean cover of the tree layer calculated as a sum of cover of particular species decreased from 61.56 ± 7.84 to $45.33 \pm 16.56\%$,

but on the other hand, the mean cover of the shrub layer increased from 0.67 ± 1.32 to $4.78 \pm 5.40\%$. The cover of tree- and shrub layers in other two forest communities was stable except of an increase of the

Table 3
Changes in species number per sample plot^a

Community	Mean no. of species		No. of ranks 1970s–1999		Z	P
	1970s	1999	Negative	Positive		
<i>Calamagrostio-Piceetum</i>						
Field layer	8.67	9.56	6	2	–1.354	n.s.
Ground layer	3.67	4.78	4	3	–1.364	n.s.
All layers	14.00	16.44	7	1	–2.263	0.024
<i>Bazzanio-Piceetum</i>						
Field layer	5.40	6.80	7	3	–1.698	n.s.
Ground layer	7.20	9.80	8	1	–2.561	0.010
All layers	14.10	18.50	10	0	–2.809	0.005
<i>Sphagno-Piceetum</i>						
Field layer	10.89	15.22	6	3	–1.899	0.058
Ground layer	4.78	7.22	7	1	–2.040	0.041
All layers	17.78	25.11	7	1	–2.316	0.021

^a Z statistics and significance probability (P) refers to two-tailed Wilcoxon signed-rank test. All significant results indicate increase of species number. Tree and shrub layer were not analysed separately due to small number of species, but they were included in the “all layers” category. n.s. = $P > 0.05$.

Table 4

Differences in diversity calculated as Shannon–Wiener index H' between original and new records^a

Community	Mean H'		No. of ranks 1970s–1999		Z	P
	1970s	1999	Negative	Positive		
<i>Calamagrostio-Piceetum</i>	0.392	0.649	9	0	–2.666	0.008
<i>Bazzanio-Piceetum</i>	0.613	0.786	8	2	–2.191	0.028
<i>Sphagno-Piceetum</i>	0.515	0.827	8	1	–2.547	0.011

^a Z statistics and significance probability (P) refers to two-tailed Wilcoxon signed-rank test. All results indicate increase of diversity.

Table 5

Changes in vegetation cover of all layers calculated as the sum of cover of particular species^a

Community	Mean cover		No. of ranks 1970s–1999		Z	P
	1970s	1999	Negative	Positive		
<i>Calamagrostio-Piceetum</i>						
Tree layer	61.56	45.33	1	7	–2.035	0.042 ^b
Shrub layer	0.67	4.78	6	0	–2.264	0.024 ^c
Field layer	103.22	106.56	3	6	–0.059	n.s.
Ground layer	9.89	26.00	7	2	–2.073	0.038 ^c
<i>Bazzanio-Piceetum</i>						
Tree layer	70.80	54.60	1	6	–1.362	n.s.
Shrub layer	1.20	3.00	5	2	–1.052	n.s.
Field layer	12.60	46.20	10	0	–2.805	0.005 ^c
Ground layer	38.60	76.30	9	1	–2.601	0.009 ^c
<i>Sphagno-Piceetum</i>						
Tree layer	30.89	33.22	4	1	–0.677	n.s.
Shrub layer	4.89	14.11	5	0	–2.032	0.042 ^c
Field layer	62.67	88.89	7	2	–2.192	0.028 ^c
Ground layer	83.33	66.89	4	5	–0.770	n.s.

^a Z statistics and significance probability (P) refers to two-tailed Wilcoxon signed-rank test, n.s. = $P > 0.05$.

^b Indicates decrease of cover.

^c Indicates increase during analysed period.

shrub-layer cover of the *Sphagno-Piceetum* from 4.89 ± 4.70 to $14.11 \pm 11.05\%$.

Cover increase in either field- or ground layer was found in all three communities (Table 5). The *Bazzanio-Piceetum* showed the most marked changes, its field-layer cover increased from 12.60 ± 6.29 to 46.20 ± 15.46 and its ground layer from 38.60 ± 25.18 to 76.30 ± 13.17 .

4.5. Indirectly estimated ecological factors

Comparison of environmental conditions between the original and new records have been done for five

factors (see methods) and two (field and ground) vegetation layers. Significant shift of environmental factors based on mean sample of Ellenberg's values was found only for light (towards heliophilous species of field layer in *Calamagrostio-Piceetum*) and for soil acidity (towards more acidic soils at species of ground layer in *Sphagno-Piceetum*). To visualise the general shift of environmental factors, we plotted species indicator values against the species scores on the first RDA axis. However we have not found any correlation between species scores and species indicator values for any community. The results are not displayed with respect to a long list of analyses and only two significant results.

5. Discussion

5.1. Problems with relevés resampling and changes evaluation

Several problems, which may strongly influence the results of further analyses and interpretation of results, must be solved in studies dealing with relevés sampled repeatedly over time: (i) inaccurate position of resampled relevés with respect to the position of original relevés; (ii) different interpretation of the degree of cover by different investigations (including use of different scales); (iii) overlooking of species, etc.

Thus, according to Malmer et al. (1978), every study on permanent plots repeated after 30–50 years will be subject to criticism that the data are not fully comparable because no person can repeat any investigation without mistakes after such a long period.

Some inadequacies can be partly removed. For example, inaccurate position can be addressed by making several records in the neighbourhood of the approximately localised old relevé, which include most of the non-homogeneity of a given stand. However this approach could seriously complicate interpretation of the results. Different values can be transferred by some, not exactly precise way to one scale (see van der Maarel, 1979). Other factors, e.g. the different subjective estimation of abundance and cover, or overlooking of species by different authors cannot be quantified but do not cause systematic bias in ordination analysis as it is quite insensitive to sampling errors (Lepš and Hadincová, 1992).

As mentioned above, we cooperated with the author of the original relevés, J. Sofron, during the repeated recording. Thus, we largely eliminated problems with the cover grades used and their interpretation. We also decided to rely on Sofron's localisation, and on the site of the original relevé we took only one record (a procedure usually used in evaluation of permanent plots). We are aware of the danger of misinterpretation. The variability interpreted as time changes could also include (mostly due to inaccurate localisation) spatial heterogeneity of vegetation. However, we believe that cooperation with the author of original relevés was sufficient to diminish the risk of an uncertain location of the individual relevés. Nevertheless, all observed changes should be evaluated with respect to the above-mentioned sampling problems.

5.2. Vegetation changes

Direct gradient analysis (RDA) confirms changes in species composition after about 30 years; however, displacement of plots along both DCA axes seems to be chaotic (Fig. 3) and does not indicate any general trend.

On the other hand, changes in frequency and cover of particular species and changes in species richness and diversity are remarkable and can indicate a shift of environmental conditions.

Only two main cumulative factors are displayed in two-dimension space of the DCA ordination diagram, other factors can be hidden there. Unfortunately, no direct measurement of environmental characteristics has been done within sampling of the original relevés. Therefore, only indirect estimation of ecological factors using Ellenberg's values was performed. Many comparisons between the two records have been done based on mean sample value for different factors and different vegetation layers. Only two comparisons yielded significant differences and indicated an increase in light penetration into climax spruce forests and increased acidity of *Sphagnum*-rich spruce forest. No other shifts of environmental conditions were confirmed by these analyses. Indirect measurement of environmental factors must be considered while interpreting these results. In practice, the indicator values of Ellenberg's implicitly defined scale seem to work well, but this type of environmental calibration does not include the interaction effect of other factors (Ter Braak and Gremmen, 1987) and could significantly differ from real site conditions. For example, for *Vaccinio-Piceetea*, Wamelink et al. (2002) found a negative relationship between Ellenberg's *R* values and soil acidity while a positive relationship was expected. Comparison of individual species response and mean sample indicator values can therefore yield inconsistent results.

From a statistical point of view, we have also to be aware of a low power of all performed tests due to low number of samples.

Based on the analysis of indicator values, changes in light conditions seem to be the most important factor observed in climax spruce forests. This hypothesis is also supported by a significant decrease in tree-layer cover in these stands which can be attributed to

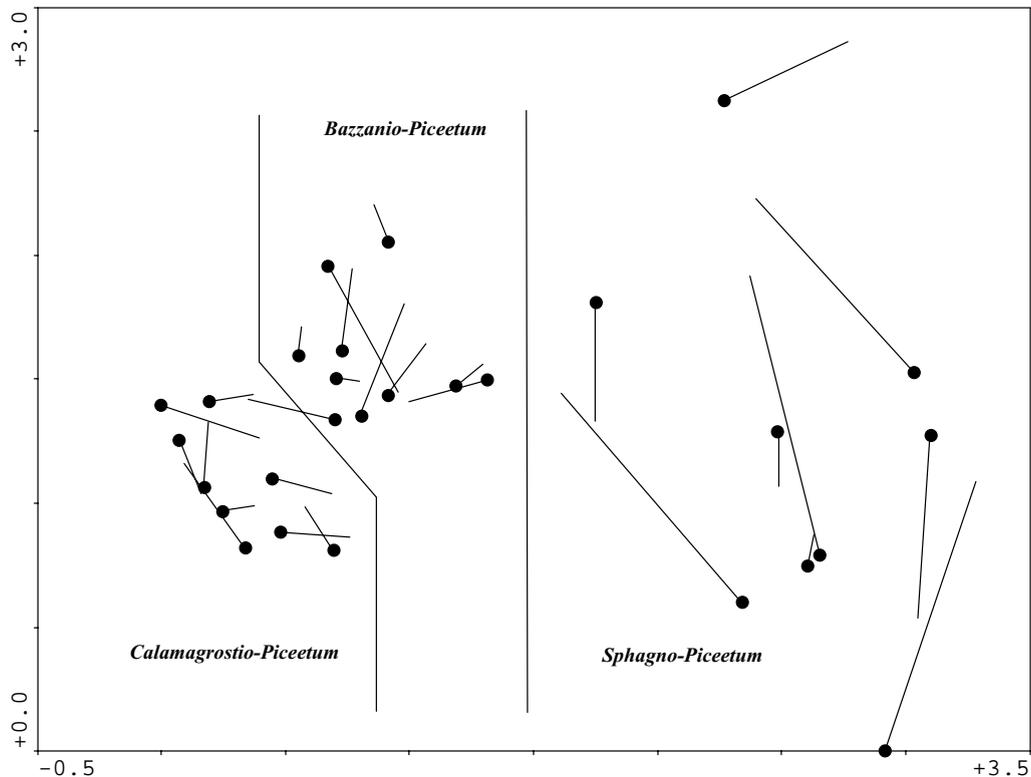


Fig. 3. Shifts in plot position in ordination space (DCA) from 1970s to 1999. Position of relevés from 1970s is indicated by dots; lines show replacement during analysed period.

wind and snow disturbances in the last few decades (Sofron, 2000, ms.), to the aftermath of bark-beetle attack and rapidly progressing defoliation since 1992 (see Zelenková et al., 2000). Changes in particular species cover and frequency indicate improved light conditions and decline of hygrophilous and sciophilous species like *O. acetosella*, and increased cover and frequency of *D. dilatata*, a species of open stony slopes at lower altitudes of the spruce-forest belt in the Bohemian Forest. Similar to the Krkonoše Mountains (Vacek et al., 1999), dominant species of the field layer (*C. villosa*, *A. flexuosa*, *V. myrtillus*) increase their cover with the loss of canopy foliage in the Bohemian Forest. However, in the Krkonoše Mountains, the canopy changes were caused directly by pollution stress. Nygaard and Ødegaard (1999) considered the changes in canopy and consequent changes in light availability as the most important ecological factor causing long-term changes in south boreal coniferous forests. However, no changes in

light indicator values and/or in tree-layer cover were observed in the two waterlogged spruce forests of the Bohemian Forest. Changes in Ellenberg's mean sample values indicated only increased soil acidity but this conclusion was drawn from analysis of ground layer species — mainly bryophytes — which possess a lower predicative value with respect to Ellenberg's values than vascular plants (cf. Düll in Ellenberg et al., 1992).

Further explanation can be derived from the dynamics of individual species. The RDA analysis (Appendix A) presents good information on increasing or decreasing species abundance or cover during the analysed period. For example, higher frequency of *A. flexuosa*, higher dominance and/or frequency of *C. villosa* and *V. vitis-idaea* in waterlogged spruce forests, as well as the frequent regeneration of *S. aucuparia* in the *Bazzanio-Piceetum* give evidence of decreasing soil moisture. The opening of spruce canopies indicated by a decrease of tree-layer cover was

not confirmed. Also, the newly occurring species in the *Sphagno-Piceetum*, also partly in the *Bazzanio-Piceetum*, indicate the tendency towards drier sites: from the meadow species — *Anthoxanthum odoratum*, *Calluna vulgaris*, *Festuca rubra*, *Luzula multiflora*, *Dactylorhiza fuchsii*, from the forest species — *S. aucuparia*, *Soldanella montana*, *B. carpatica*, *Hieracium lachenalii*.

A higher dominance of *E. vaginatum* and *Oxyccocus palustris* in waterlogged spruce forests of the Bohemian Forest does not contradict the hypothesis on soil moisture reduction — it is evidence to more suitable moisture conditions in former strongly waterlogged stands of the *Sphagno-Piceetum* with reduction of excessive soil moisture in the last 30 years and a certain retreat of *C. rostrata*.

The only general trend found — a significant shift to species-rich communities and to higher diversity — was observed in all communities studied. The most remarkable and striking shift was found in the *Sphagno-Piceetum*. These results are in contradiction with other authors who, recorded species-poor types. These authors explained the decrease of species richness, for example, by pollution stress (Vacek et al., 1999) or by increased canopy cover (Nygaard and Ødegaard, 1999). However these factors are either of low importance (pollution stress) or were even excluded (canopy increase) in our study plots. Some small changes can be explained by short-term variability (cf. Økland, 1995; Økland and Eilertsen, 1996). Changes in bryophytes and lichens can be partly attributed to wrong determination by some authors (especially *Sphagnum* or *Calypogeia* species), overlooking (*Pohlia* and *Cephalozia* species), and/or local disturbances (e.g. *Mylia anomala*, *Dicranella heteromalla*). However, such a marked increase in species number as in the *Sphagno-Piceetum*, especially in higher plants (14 species more in total and 4.33 more per relevé in average) cannot be explained by any of the above-mentioned factors.

The increasing number of vascular plants can be linked to chemical changes in the atmosphere during the last ≈10–15 years. First atmospheric acidification records in the Bohemian-Forest lakes date between 1959 and 1961, with the heaviest impact culminated around 1980 (Vrba et al., 2000), which corresponded with the time of collection of the first lot of relevés. During the last 15–10 years, the amount of sulphur

dioxide in wet depositions dropped markedly as well as the content in Bohemian-Forest lakes (Veselý, 1996). Also, Kopáček et al. (2001) mentioned a fall in atmospheric acidification of the Bohemian-Forest lakes from the second half of the 1980s. Thus, pH of the Bohemian-Forest lakes rose since the 1980s, e.g. in the Bavarian lakes (Kleiner Arbersee, Rachelsee) it increased from 4.3 in 1983 to 4.8 in 1999 (Schaumberg, 2000). This trend probably influenced the increase in both abundance and diversity of algae and other phytoplankton in some lakes. Mánek (1998) also mentioned the dependence of species diversity of riverside vascular plants on the chemistry of Bohemian-Forest waters. Lower pollution stress in Bohemian Forest compared with other mountains was also observed by Sucharová and Suchara (2001).

This explanation is in contradiction with the predicted increase of acidity in waterlogged forests. However, this finding is based on debatable and indirect measurement only (see above) and was significant for one community and one species group (bryophytes) only. It cannot compete with proof of decreasing acidity from direct measurement of pollutant contents by several authors. Rather it suggests the doubtful use of Ellenberg's values than on conflicting trends in acidity.

Climate warming is an alternative explanation of species richness increase and shift to drier types. We can observe frequent attempts to shift forest vegetation belts to higher altitudes (e.g. Brzeziecki et al., 1995; Majer, 2001; Neuhäuslová, 2001; Vacek and Mayová, 2000; Vinš et al., 1996; Buček and Kopecká, 2001, etc.). As a result of global warming, the retreat of spruce forests from the Šumava National Park and their replacement by mountain spruce–beech forests is to be expected in the near future, around the year 2010, according to Vinš et al. (1996) and Buček and Kopecká (2001). This prediction, together with prediction of soil moisture decrease, could be supported by the comparison of waterlogged spruce forest area on the Geobotanical Map of the Czech Republic compiled at the beginning of the second half of the last century (Mikyška, 1968–1972) with the Map of Potential Natural Vegetation of the Bohemian Forest (Neuhäuslová et al., 2002). It is unrealistic to suppose that the remarkable reduction of the spruce forest area on the Map of Potential Natural Vegetation of the Šumava National Park was due to concept differences

in mapping units between the different authors of the same mapping school.

Differences in climatic data measured during several decades and more frequent dry periods also show certain shifts to a warmer climate (cf., e.g. Staněk (2002) or data from the climatic stations at Březník, etc. depon. in: Administration of the National Park and Protected Landscape Area, Bohemian Forest).

Fragmentation of forests resulting from bark-beetle attacks and subsequent forest clearcut must also be considered as one of the possible sources of increasing species richness. Many new clearings can serve as a source of species, which can invade drying stands in waterlogged spruce forests.

None of the hypotheses discussed in relation to waterlogged forests (decrease of atmospheric acidification, global warming or forest fragmentation) is in contradiction with observed species changes in climax spruce forest. However, since all these hypotheses cannot be confirmed by our data we suggest that the main factor responsible for changes observed in climax spruce forest is a pronounced decrease of canopy cover.

It is necessary to mention specific cases when species changes cannot be related to changes in the stands analysed. For example, the recent invasive species *G. saxatile* points to its current spreading on suitable, more-or-less open fresh to moist sites on mountain clearings and in open forests in Bohemian Forest since the first half of the 20th century (cf. Slavík, 2000: 150). The decline of chionophilous species *A. distentifolium* in the living forest on the northern side of the Jezerní Mountain is hard to explain, because this species has been growing there on extensive clearing at a distance of ca. 0.5 km to the NW with high dominance and vitality. A similar, fairly hardly explicable phenomenon was mentioned by Petermann and Seibert (1979) from the neighbouring Bavarian Forest, National Park Germany, and by Krahulec (in litt.) from the Hrubý Jeseník Mountains. It was not possible to prove if the cause was due to a change in local snow conditions or other factors.

6. Conclusion

The dynamics of coniferous stands in the Bohemian Forest have been studied based on repeated sampling

of 28 forest stands classified to three communities (climax spruce forests — *Calamagrostio-Piceetum* and waterlogged spruce forests — *Bazzanio-Piceetum* and *Sphagno-Piceetum*). Significant changes in species composition have been confirmed. However, ordination analysis over all plots did not detect any common trends in all the communities. Species turnover and changes in cover and frequency of particular species indicated a tendency towards communities of open and/or drier vegetation types. Also, the shift to more species-rich communities has been found in all the vegetation layers analysed (tree, shrub, field and ground). The most remarkable shift was detected in waterlogged stands. The single direct factor, decrease in canopy cover, together with more complex factors — decrease of air pollution, forest fragmentation or global warming — were discussed as possible explanations for the changes observed.

Acknowledgements

The authors thank the Grant Agency of the Czech Republic for financial support (grant project 206/96/1416). This study was also supported by the grant project AVOZ 6005908. Our thanks to B. Buryová and H. Franklová for determination of bryophytes and to V. Eltsova for data entry. P. Pyšek and M. Kovářová read and criticised the draft of this paper. Thanks are due to the both anonymous reviewers for many helpful comments on an earlier version of this contribution.

Appendix A

Species exchange survey. The first column gives species scores on the first axis of RDA analysis. The scores indicate correlation of species cover with time: cover of species with positive value increases and vice versa. The columns labelled by date give occurrence frequency in corresponding years. The last three columns refer to percentage number of plots where the species retreated, occurred in 1970s and persisted in 1999 and emerged, respectively. Percentage numbers are related to the total number of plots where the species occurred in either 1970s or 1999. Only species occurring in three or more relevés in any one of the time are included. Shrub and tree layers are marked

with abbreviation: sl—shrub layer, tl—tree layer.

<i>Calamagrostio-Piceetum</i>	First axis scores	1970s	1999	Retreated	Persisted	Emerged
<i>Picea abies</i>	0.615	7	9	0	100	22
<i>Picea abies</i> -sl	0.470	1	5	0	100	80
<i>Galium saxatile</i>	0.427	0	3	0	0	100
<i>Dicranum scoparium</i>	0.381	6	7	17	83	29
<i>Dryopteris dilatata</i>	0.379	9	9	0	100	0
<i>Sphagnum girgensohnii</i>	0.302	4	5	0	100	20
<i>Luzula sylvatica</i>	0.282	6	6	0	100	0
<i>Plagiothecium laetum</i>	0.267	1	3	0	100	67
<i>Sorbus aucuparia</i> -sl	0.260	1	3	0	100	67
<i>Sorbus aucuparia</i>	0.255	6	6	33	67	33
<i>Homogyne alpina</i>	0.228	4	6	25	75	50
<i>Trientalis europaea</i>	0.216	4	6	25	75	50
<i>Dicranodontium denudatum</i>	0.167	1	3	0	100	67
<i>Vaccinium myrtillus</i>	0.160	5	7	0	100	29
<i>Rhytidiadelphus loreus</i>	0.116	3	2	33	67	0
<i>Barbilophozia lycopodioides</i>	0.093	4	4	25	75	25
<i>Polytrichum formosum</i>	0.074	6	7	17	83	29
<i>Avenella flexuosa</i>	0.058	9	9	0	100	0
<i>Calamagrostis villosa</i>	0.000	8	9	0	100	11
<i>Sorbus aucuparia</i> -tl	0.000	3	2	67	33	50
<i>Polytrichum commune</i>	0.000	2	1	50	50	0
<i>Maianthemum bifolium</i>	-0.098	5	3	40	60	0
<i>Lycopodium annotinum</i>	-0.149	2	1	50	50	0
<i>Oxalis acetosella</i>	-0.272	7	5	43	57	20
<i>Athyrium distentifolium</i>	-0.329	3	1	100	0	100
<i>Picea abies</i> -tl	-0.557	9	9	0	100	0
<i>Bazzanio-Piceetum</i>	First axis scores	1972/1974	1999	Retreated	Persisted	Emerged
<i>Picea abies</i>	0.706	9	10	0	100	10
<i>Vaccinium myrtillus</i>	0.651	10	10	0	100	0
<i>Dicranum scoparium</i>	0.582	8	10	0	100	20
<i>Ptilidium ciliare</i>	0.500	0	4	0	0	100
<i>Bazzania trilobata</i>	0.473	10	10	0	100	0
<i>Dicranodontium denudatum</i>	0.446	5	9	0	100	44
<i>Picea abies</i> -sl	0.388	3	7	33	67	71
<i>Vaccinium vitis-idaea</i>	0.383	4	5	0	100	20
<i>Sorbus aucuparia</i>	0.376	4	7	25	75	57
<i>Avenella flexuosa</i>	0.326	5	8	0	100	38
<i>Lycopodium annotinum</i>	0.320	3	4	0	100	25
<i>Dryopteris dilatata</i>	0.313	4	6	25	75	50
<i>Sphagnum magellanicum</i>	0.288	3	5	0	100	40
<i>Calamagrostis villosa</i>	0.278	8	7	25	75	14
<i>Homogyne alpina</i>	0.226	1	2	0	100	50
<i>Tetraphis pellucida</i>	0.218	2	4	0	100	50
<i>Polytrichum formosum</i>	0.215	6	8	0	100	25

Appendix A. (Continued)

<i>Bazzanio-Piceetum</i>	First axis scores	1972/1974-1999		Retreated	Persisted	Emerged
<i>Sphagnum girgensohnii</i>	0.201	5	8	0	100	38
<i>Eriophorum vaginatum</i>	0.196	1	2	0	100	50
<i>Pleurozium schreberi</i>	0.169	1	3	100	0	100
<i>Polytrichum commune</i>	0.135	3	4	67	33	75
<i>Calypogeia integristipula</i>	0.113	2	2	100	0	100
<i>Sphagnum russowii</i>	0.038	3	4	33	67	50
<i>Anastrepta orcadensis</i>	0.000	2	1	50	50	0
<i>Lepidozia reptans</i>	0.000	2	2	50	50	50
<i>Rhytidiadelphus loreus</i>	0.000	2	2	50	50	50
<i>Dicranum fuscescens</i>	−0.109	2	3	50	50	67
<i>Cephalozia lunulifolia</i>	−0.316	3	0	100	0	0
<i>Sphagnum capillifolium</i>	−0.344	3	1	67	33	0
<i>Picea abies-t1</i>	−0.380	10	10	0	100	0
<i>Sphagno-Piceetum</i>	First axis scores	1972/1974-1999		Retreated	Persisted	Emerged
<i>Picea abies-s1</i>	0.5835	7	9	0	100	22
<i>Avenella flexuosa</i>	0.5092	1	5	0	100	80
<i>Vaccinium vitis-idaea</i>	0.4333	9	9	0	100	0
<i>Betula pubescens agg.-t1</i>	0.4272	0	3	0	100	67
<i>Polytrichum commune</i>	0.4151	7	8	0	100	13
<i>Trientalis europaea</i>	0.3101	6	6	17	83	17
<i>Calamagrostis villosa</i>	0.2580	5	8	0	100	38
<i>Agrostis stolonifera</i>	0.2563	1	2	0	100	50
<i>Vaccinium uliginosum</i>	0.2485	3	5	33	67	60
<i>Molinia caerulea</i>	0.2357	1	2	0	100	50
<i>Vaccinium myrtillus</i>	0.2279	8	9	0	100	11
<i>Homogyne alpina</i>	0.2195	2	4	50	50	75
<i>Carex echinata</i>	0.2085	2	3	50	50	67
<i>Oxycoccus palustris</i>	0.1951	5	6	40	60	50
<i>Carex nigra</i>	0.1723	5	8	0	100	38
<i>Eriophorum vaginatum</i>	0.1721	5	8	0	100	38
<i>Crepis paludosa</i>	0.1491	1	2	0	100	50
<i>Betula carpatica</i>	0.1435	2	1	100	0	100
<i>Melampyrum pratense</i>	0.1374	5	6	20	80	33
<i>Viola palustris</i>	0.0995	2	2	50	50	50
<i>Sphagnum magellanicum</i>	0.0833	3	5	33	67	60
<i>Dicranum scoparium</i>	0.0819	2	3	100	0	100
<i>Picea abies-t1</i>	0.0624	9	9	0	100	0
<i>Picea abies</i>	0.0586	6	6	17	83	17
<i>Aulacomnium palustre</i>	0.0354	1	2	100	0	100
<i>Equisetum sylvaticum</i>	0.0000	2	2	50	50	50
<i>Polytrichum strictum</i>	0.0000	2	3	0	100	33
<i>Carex rostrata</i>	−0.0201	3	4	0	100	25
<i>Drosera rotundifolia</i>	−0.0671	1	3	0	100	67
<i>Potentilla erecta</i>	−0.0819	5	4	40	60	25

Appendix A. (Continued)

<i>Sphagno-Piceetum</i>	First axis scores	1972/1974	1999	Retreated	Persisted	Emerged
<i>Pleurozium schreberi</i>	−0.0885	6	6	33	67	33
<i>Bazzania trilobata</i>	−0.0995	2	2	0	100	0
<i>Juncus effusus</i>	−0.1200	2	2	100	0	100
<i>Sphagnum fallax</i>	−0.2416	6	6	50	50	50
<i>Sphagnum russowii</i>	−0.2964	3	6	33	67	67
<i>Deschampsia cespitosa</i>	−0.3982	3	1	100	0	100

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